THE EXPLOSIVE DEVELOPMENT OF A FLOATING WEED VEGETATION ON LAKE KARIBA

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Abstract:

The occurence on Lake Kariba of floating weed mats, formed in the first instance by the introduced water-fern *Salvinia auriculata*, is described.

A further colonisation of these weed mats by 40 species of vascular plants in a process of sudd formation is illustrated.

The implications of this water infestation on the lake and its possible origin and future behaviour are discussed.

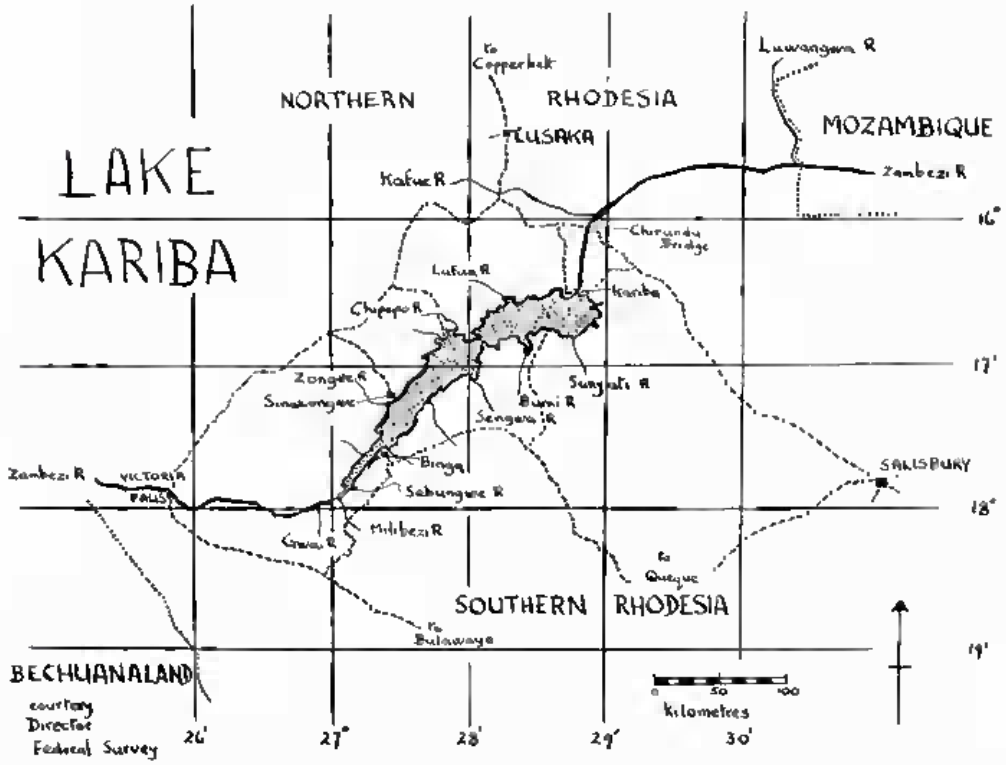
INTRODUCTION

The larger rivers of Africa, representing the world's greatest inland water resource, have until this last decade remained largely unexploited as sources of electric power. The biological problems arising from the creation in these rivers of hydro-electric storage dams have therefore not yet been generally experienced. The establishment of what is at present the largest man-made lake in the world by damming the Zambezi River, in its course between Northern and Southern Rhodesia, has provided a dramatic and instructive illustration of the biological events which may follow the inception of such a hydro-electric project.

The Kariba scheme called for the construction of a dam at the entrance to the Kariba Gorge which would create a storage reservoir some 280 km. long by 80 km. wide and covering approximately 440,000 hectares, reaching its operative level during the 1960's. The Kariba Dam was closed on December 2nd. 1958, thus containing the 1958-59 flood, which started to flow about the beginning of December, and reached its maximum in March and April 1959. The impounding of the Zambezi waters thus resulted about the end of April of that year in the creation of a temporarily stable embryo lake whose level was far higher than that of any previously recorded flood. In the May of this natal year 1959 the first reports of floating weed mats on the new lake started to come in. Weed specimens seen by Dr. E. A. C. L. E. Schelpe, then working in

England and reviewing the ferns for the Flora Zambesiaca, were determined by him as *Salvinia auriculata* Aublet.

This *Salvinia* species was described by AUBLET from Guiana. It is widely distributed in Central and South America, and the Caribbean area. *S. auriculata* is readily distinguished from the one other *Salvinia*



species found on the eastern side of Tropical Africa and in Madagascar, *Salvinia hastata* Desv., by the fact that the latter species has simple instead of branched hairs on the upper surface of the leaves, more correctly termed fronds (Hertzog 1935).

ADAMSON (1950) recorded *S. auriculata* from the Cape area of South Africa more than ten years ago. Aecording to SCHELPE (1961) it now also oecurs in the Knysna district and a few other localities in the Republie, although in his classic ecological account of the Knysna region, PHILLIPS (1931) does not record the presence of the fern. A specimen later determined as *S. auriculata* was collected by Dr. O. WEST in the Zambezi a little way above the Victoria Falls in 1949. Subsequently the fern also appeared in farm dams, once in Kenya and twiee in Southern Rhodesia. Elsewhere, WILLIAMS (1956) gives an account of an outbreak in the rice paddies and natural waters of the eastern seabord of Ceylon.

SALVINIA ON LAKE KARIBA

The mats of floating water-fern first reported in May 1959 from the central section of the lake continued to increase in size and number all through that year, until a fringe of *Salvinia* bordered both shores of the lake from near Binga upstream to the Bumi River confluence in the Lower Basin. At this time the *Salvinia* mats were fairly pure, the only other plant associated with them being *Pistia stratioles* L., still in small amount.

Salvinia auriculata plants have two distinct growth phases, which has sometimes in the past led to taxonomic confusion. The first stage, termed 'primary', is a sterile vegetative phase in which the leaves of the plants are more or less flat, and all of them float out over the water surface (photo 1). The 'tertiary' phase (photo 2) develops by a further growth and a folding together of the upper surfaces of the two halves of each leaf, and a renewed growth of the third modified leaf associated with each pair of photosynthetic leaves, which is adapted to form a root-like structure, and on which micro- and mega-sporangia now proceed to develop. The younger and more distal portions of the plants in this tertiary stage are supported above the surface of the water by the moribund and submerged older portions, which are buoyed up by the air trapped between the hairs of their now folded upper leaf surfaces. The greater portion of the *Salvinia* on the lake is in this tertiary stage, which is said to be initiated as a result of the crowding together of *Salvinia* plants in the primary stage. The 'secondary' growth stage of the fern, intermediate between the primary and the tertiary, is transitory and is not commonly encountered.

Vegetative reproduction, the only form of propagation so far observed on the lake, occurs when additional shoots formed on the original fern plant by growth from lateral buds, become detached from the parent plant.

The floating mats of *Salvinia* are very subject to dispersal or transport by the wind, even in the primary stage when the amount of the plant emerging above the surface of the water can be only a few millimetres. As soon as a substantial degree of flooding had occurred in 1959, crowns of trees which had been only partially submerged on the temporary shores of the new lake offered some protection from these disturbing winds, and some catchment to lodge the *Salvinia* plants and prevent their being blown away. The weed infestation in the second half of 1959 therefore tended to be around the treed shores. There was already however a considerable mass of weed floating free across the lake surface, sometimes as scatterred individual plants, but more usually as great arcs of interlaced plants drifting quite rapidly down-wind.

Photo 1. — *Salvinia auriculata* floating on Lake Kariba, most of the plants in the *primary* stage; three plants towards the top right hand corner in the *secondary* stage, the leaves having just commenced to grow again and to fold up.

Photo 2. — *Salvinia auriculata* floating on Lake Kariba, all the plants in the *tertiary* stage; individual plants have a worm-like appearance, the tightly packed leaves are folded, and the new growth is supported clear of the water.

By April 1960 the total mass of floating weed on the lake surface was estimated as covering some 20,000 hectares (SCHELPE 1961). That same year moreover saw the appearance of a very extensive colonisation of the hitherto almost pure *Salvinia* mats by a further complex of vascular plant species.

SUDD DEVELOPMENT ON LAKE KARIBA

Early in 1960 it became apparent that in addition to *Pistia*, a whole series of vascular plants could become established on the *Salvinia* mats. Because of the similarity of these weed colonies which now formed to the floating masses of vegetation in the swamps of the Upper Nile, I termed these 'sudd' colonies, despite the absence of *papyrus*. Up to the end of 1961 I had found a total of 40 vascular plant species growing on the floating weed mats, and these are listed in the table below. Only one of these species *(Vossia)* is apparently able to survive in the form of free-floating colonies, more than temporary periods isolated from the support of the *Salvinia* mat.

This list of species does not include the few ephemeral but spectacular appearances of certain cultivated plants and tree seedlings. In 1960 well advanced banana plants standing out of the *Salvinia* mats were a not uncommon sight, although none were recorded to have reached the fruiting stage or appeared again in subsequent years. These bananas must have grown from suckers floating up from the flooded Tonga cultivations now below the waters of the lake. The same source would account for the frequent luffa (*Luffa cylindrica* Roem.) colonies, which still continue happily to complete their life-cycle and perpetuate themselves on the weed mats. Large quantities of tree seedlings also appeared locally in 1960, but only rarely later, coming especially from two species, *Acacia albida* Del. and *Colophospermum mopane* (Kirk ex Benth.) Kirk ex Leonard. The first species grew commonly in the riparian forest of this area along the Zambezi, and continued to fruit even when at least half-submerged, like the date palms inundated by the Aswan Dam in Egypt. The *mopane* seedling came from seed produced by the multitude of trees of this species, which is the dominant tree of the flatter and lower areas of the Zambezi Valley in this region. Seedlings of a *Ficus* sp. were also observed; no tree seedlings of any species survived more than a few months on the weed mats.

The more permanent weed mat colonisers appear to fall into two groups, those of semi-aquatic habitats, and ruderals of open ground generally. Among the former are the species of *Ludwigia*, *Polygonum*, *Cyperus*, *Scirpus*, *Typha* and *Phragmites mauritianus*. Among the ruderals are *Eclipta alba*, *Alternanthera nodiflora* and *Commelina diffusa*.

ORIGIN OF SUDD SPECIES

Without exception, no species so far recorded as occurring in association with sudd colonies, whether an introduced ruderal or an indigenous semi-aquatic plant, cannot be found growing elsewhere in some part or other of the Zambezi drainage system. Indeed very much more might have been predictable as to the possibilities of sudd formation on the lake if more had been known beforehand of swamp ecology in this and other adjacent territories.

A somewhat similar complex of semi-aquatic species forming floating mats has been described from the adjoining Congo by LEONARD (1952) and by GERMAIN (1952). LEONARD describes a floating aquatic association in stagnant water on the Congo River at Yangambi, composed of *Pistia stratioles*, *Azolla pinnata* and *Lemna paucicostata* as dominants, which becomes invaded by *Ipomoea aquatica* and *Jussiaea repens*, together with a few other associates including *Commelina diffusa*. Under the class of herbaceous semi-aquatic vegetation LEONARD also has associations, of which his *Jussiaea repens* and *Enhydra fluctuans* association, forming a floating mat in the still or slightly moving water of creeks, containing among other species *Commelina diffusa*, *Jussiaea repens*, *Cyperus mundtii*, *Scirpus cubensis*, together with *Pistia stratioles* and *Azolla pinnata*, closely resembles the Lake Kariba sudd.

GERMAIN defines a *Cyperus latifolius* association which includes *Jussiaea suffruticosa*, *Ageratum conyzoides*, *Typha angustifolia* subsp. *australis*, *Polygonum* spp and a *Vigna* sp.

This is not the place to review all the literature on this subject, but it is apparent that floating colonies of swamp plants are widely distributed in Tropical Africa, even as far north as Senegal. There TROCHAIN (1940) records an *Echinochloa stagnina* and *Vossia cuspidata* group which includes *Pistia stratioles*, *Cyperus auricomus*, *Scirpus cubensis*, *Jussiaea villosa*, *J. linifolia*, *J. desruia*, *Polygonum lanigerum*. In a later paper, detailed comparisons will be made between the sudd on Lake Kariba and the floating swamp associations such as these which have been described by a number of ecologists throughout Africa. A review of this work does suggest the possibility that in natural waters in Africa *Azolla* species may have played the same pioneering role, providing a mat for further colonisation, that *Salvinia auriculata* has served in the artificial waters of Lake Kariba.

The nearest area of extensive natural swamp to Lake Kariba is the Lukanga Swamps, some distance west of Lusaka in Northern Rhodesia, where the river Lukanga runs into the Kafue River, a tributary of the Zambezi. Dr. S.C. SEAGRIEF visited this swamp in 1958, and his collection of plants is deposited in the Central African Herbarium at the University

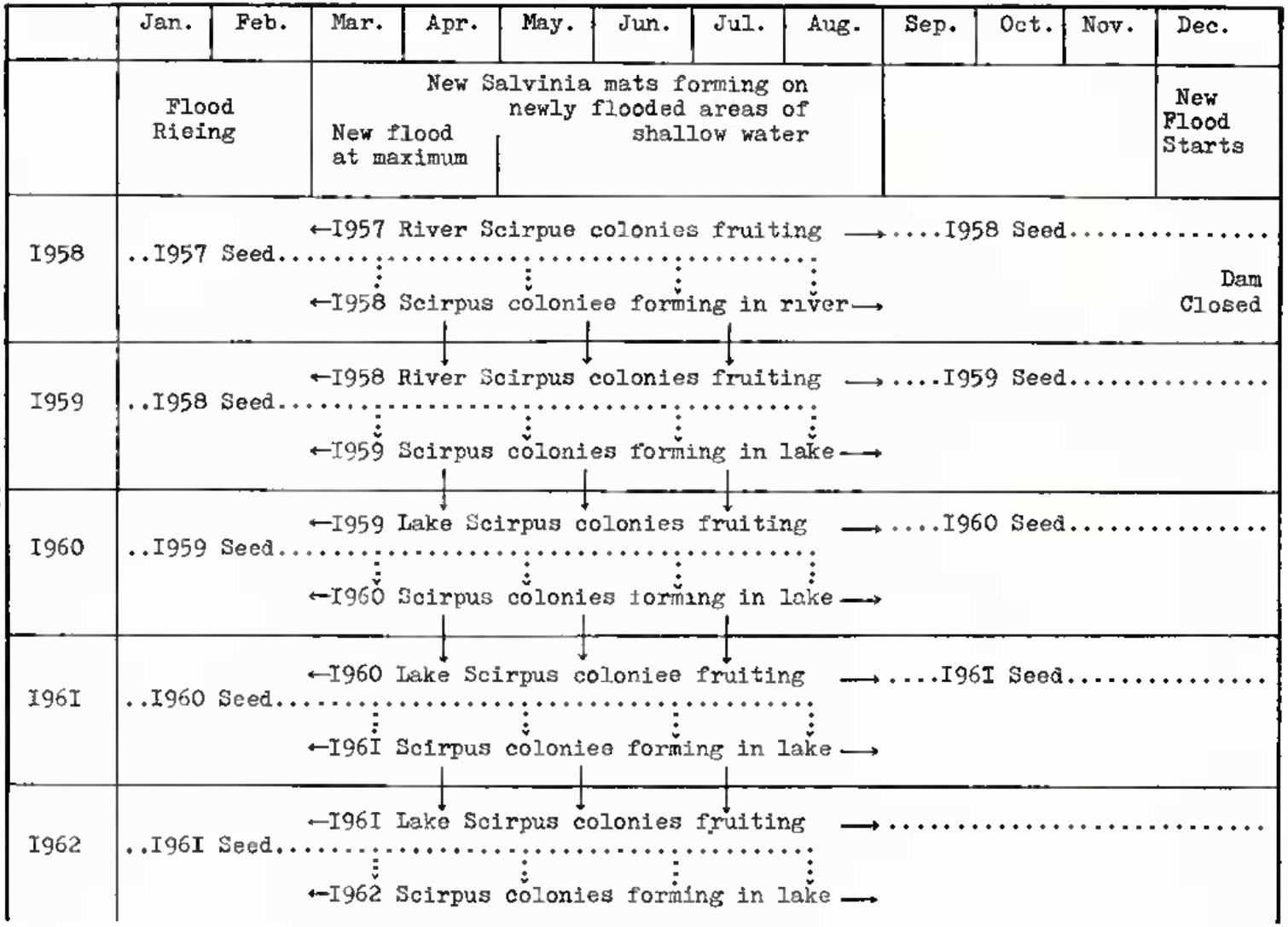
College. The annotations made on his specimens at the time now make extremely interesting reading. SEAGRIEF has recently published a note (1962) on the ecology of the swamps, in which he confirms that masses of floating vegetation are to be found in the Lukanga Swamps, and that such Kariba sudd species as *Ludwigia leptocarpa*, *Polygonum lomentosum*, *Cyperus nudicaulis*, and *Pycreus mundtii* are associated with the floating *Scirpus cubensis* mats. At the time of his visit, August 1958, *no Salvinia auriculata* was seen, suggesting that the *Scirpus* mats had a different origin from those on Lake Kariba. Although the Kafue River runs into the Zambezi downstream of the Kariba Dam, and diaspores of sudd species cannot be swept down it into the waters of the lake, there must be similar but smaller patches of the swamp described by SEAGRIEF on other tributaries of the Zambezi which feed directly into the lake. An additional source of sudd diaspores is the vegetation surrounding the freshwater springs of the valley, such as Manjolo Spring near Binga, with semi-aquatics such as *Ludwigia* spp., *Cyperus* spp., and *Typha* spp.

The source of the diaspores of the sudd ruderals seems to be the temporary vegetation which forms on the lake's 'soak zone' as the water level becomes more or less stabilised each year in the winter, with the slackening of the annual flood which has moved the lake to a new higher level. Along this soak zone ruderals such as *Eclipta alba* and *Allernanthera nodiflora* are very common, together with some of the grasses which feature in the sudd like *Panicum maximum*.

DEVELLOPMENT OF SUDD COLONIES

Observations first made in 1960 suggested that sudd clumps fall into two size groups. This indicates that sudd colony formation is not a continuous process, but occurs only at particular times of the year, despite the apparent presence of a suitable habitat for colonisation at all seasons. The diagram in fig. 1 illustrates a possible explanation for this seasonal sudd colonisation; it should be noted that this applies only to sudd formed by *Scirpus cubensis*, which is assumed to have a limited flowering season, andt o have seeds which require a dormant period of some months. It is also assumed that both *Salvinia auriculata* and *Scirpus cubensis* were present in the area of the Zambezi now flooded by the lake, or in the lower estuaries of one or more of the tributaries, before the dam was closed in 1958.

Whatever their origin and mode of development, the continuing existence of any particular sudd colony on the lake is almost entirely dependent upon its degree of exposure to wind. The action of the wind upon a weed mat produces results very similar to those of a wind-blown ice-pack. Although the weight of the weed is less than that of ice, and the forces concerned are not therefore as great, a wind-driven weed mat caught up in the crown of a half-submerged tree has been observed to snap off the trunk. The effect of this pressure in wind-driven weed mats on older sudd colonies is annihilating.



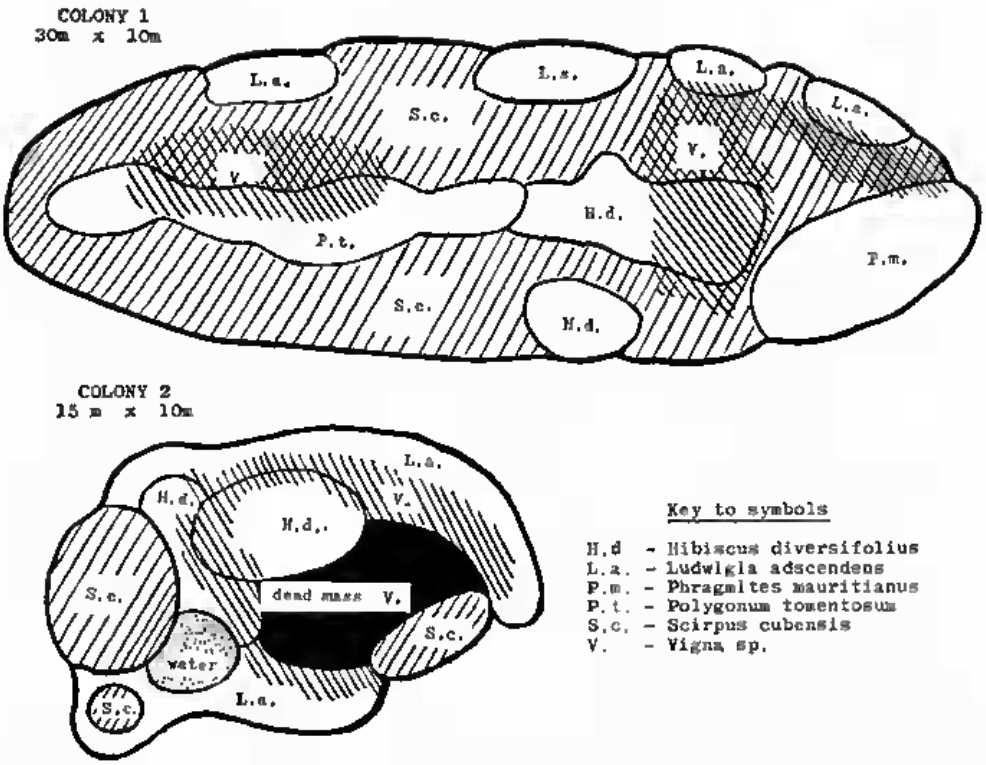
Pl. 1. — Scheme illustrating the dates of fruiting of *Scirpus cubensis* and the corresponding times of appearance of new sudd colonies on the *Salvinia* mat on Lake Kariba.

When blown before the wind, the various components of a weed mat will not move together. The *Salvinia*, offerring the least underwater resistance, will sail away first, followed closely by the *Pistia*. The smaller sudd colonies follow, the young shoots of many of these collapsing on the water when no longer supported by the *Salvinia* mat, and the young colony then presumably rotting and dying. The larger sudd colonies bring up the rear several hours, or even a day or so behind. When the drifting *Salvinia* ahead is stopped by a headland or other physical obstruction, the whole mat, or such part of it as has not sunk en route, is reconstituted, the sudd colonies working their way in to achieve a random scatter much as before the mat was disturbed in the first place.

The prevailing wind on Lake Kariba for almost all the days of the year is approximately E.N.E., that is, more or less upstream over the greater part of the lake. Before each new flood begins in December, a mass of weed mats therefore tends to accumulate near the head of the lake, and to windward of the larger north-south promontories. The weight of weed in these localities eventually becomes so great that the *Salvinia* piles up in great waves, up to two metres thick in the ridges. The uppermost *Salvinia* plants soon die, perhaps from over-heating, and those below become moribund, perhaps because of lack of light or oxygen, or accumulations of carbon di-oxide. Under these conditions the older sudd clumps fare equally badly. In their second year, those formed entirely or partly of *Scirpus rubensis* have become very loose inside, because the shoots of this species apparently die after fruiting in their second year. Such hollow colonies are easily squashed flat by the pressure of the *Salvinia* mass. Only a very few third year colonies can survive unprotected, and not many have been seen on the lake; two that were found in 1961 are illustrated in fig. 2.

There are two situations in which sudd colonies may escape the pressure of the wind-driven mats, in the lee of islands and among the half-submerged tree crowns fringing the shore. The latter situations are the more common : sudd colonies trapped in tree crowns tend to merge and form a continuous line of sudd. Between this line and the actual shore, *Salvinia* finds in this protected water ideal conditions under which to grow and multiply. Such situations are now the most important *Salvinia* 'nurseries' in the maturing lake.

The areas occupied by *Salvinia*, *Pistia* and sudd respectively are difficult to estimate. After the April 1960 estimate of 20,000 hectares of total weed mats, a survey in August 1960 gave an increase to about 30,000 hectares, according to the figures of the Lake Kariba Co-ordinating Committee. Their later estimates suggest that the weed mats continue to occupy approximately one tenth of the total water surface. How much of this is actually occupied by sudd colonies it is difficult to determine. They are never so dense in obstacle-free water that a launch power-



Pl. 2. — Sketches showing the composition and species distribution in two of the rare three-year-old sudd colonies which are to be found in the weed mats on Lake Kariba. Note that the first colony illustrated is in process of being squashed.

ful enough to push through thick *Salvinia* cannot work its way through them. Although the reproductive rate of the *Salvinia* is apparently so fantastically great that it grows away almost pure in the *Salvinia* 'nurseries', an older mat may have as high an admixture of *Pistia* as 50 per cent or even more.

FUTURE DEVELOPMENT OF THE WEED ON LAKE KARIBA

The economic development of the Lake Kariba area, as distinct from the control of the actual dam site and the hydro-electricity plant, is in charge of the Lake Kariba Co-ordinating Committee, whose officials have shown a stimulating imagination in grappling with the weed problem which was suddenly thrust upon them. Under their aegis, an independent weed-control firm from the Republic of South Africa is carrying out on the spot trials of all promising methods of weed control, especially the use of herbicides, and the possibility of biological control is under investigation by the Commonwealth Institute of Biological Control at Trinidad. Various local botanical and fisheries organisations have been made responsible for charting the actual progress of the weed and the areas

which it covers. At the University College autecological investigations on *Salvinia auriculata* have been instigated with Mr. D.S. MITCHELL in charge, and I have undertaken to study sudd colonisation. The officials of the committee work patiently through not only the many suggestions sent in as to control of the weed, but also the numerous recommendations as to its economic exploitation, which range from the production of animal and even human food to the manufacture of plastic ash-trays.

The autecological investigations will provide not only informations on the biology of *Salvinia auriculata* but also some idea of why explosive reproduction of this species has occurred on Lake Kariba, and how long this stage is likely to persist in the maturing lake. Already reproduction of *Salvinia* seems to have levelled off so that it continues to occupy one tenth of the water surface, but this is still a very considerable proportion of what is to be 440,000 hectares of water. MITCHELL's work may be able to explain why, although apparently mature micro- and megaspores are produced in great quantities, reproduction of *Salvinia* in the lake is apparently always vegetative. The relationship of the several growth stages, and the factors which control their appearance, may also be explained by these autecological studies.

Great masses of *Salvinia* are known to be present in the Upper Zambezi, but the area is too remote to permit easy access to ascertain the exact nature of this infestation, which was presumably the original site of introduction of the weed, perhaps by an enthusiastic aquarist— the plant is still listed in some aquarist's catalogues. Certainly it is known that the infestation several years ago was so great that basins in the Upper Zambezi used by the local people for communal fish drives, had to be abandoned for this purpose because of the *Salvinia* cover.

If the explosive reproduction of the fern is dependent on unusually high concentrations of nutrients, this species might find in the annual floods of the Upper Zambezi ideal conditions for its vegetative growth. It will also be significant in this respect that when the lake is operating to capacity, one third of the water will be replaced each year, mostly by such flood waters.

Salvinia has always been concentrated in the central and upper reaches of Lake Kariba. It did not reach the dam site in the lower basin until early in 1961, and it is still not extensive there, or in what is locally called the Sunyati basin, into which flows the largest tributary reaching the Zambezi on the lake. The relative scarcity of *Salvinia* in this part of the lake could be due as much or entirely to a difference in the nutrient status of the water as to the late occurrence of an infestation there, or to the removal by the wind of any free colonies. This is again a point on which the autecological investigations may throw some light.

Economically, the most important site on the lake is above all the area immediately surrounding the dam, controlled by the Federal Power Board, and where the turbine intakes are located. The fishing pitches, cleared of all woody growth at considerable expense to within a few centimetres of the ground, and the major harbours are next in importance. By the erection of a boom across the entrance to the Kariba Gorge, it has been possible for all practical purposes to keep *Salvinia* from entering the tubine intakes. The fishing pitches, having no partially submerged tree growth to hold the weed, only become covered where they are sited across the wind, or at the head of the lake where weed accumulates. Of the major harbours, Sinazongwe, the largest port on the north bank, was virtually unapproachable from the water for two years, but now like the other harbours, remains fairly clear of weed. The question therefore remains, if the *Salvinia* nurseries in the mature lake continue to function as outlined here, they should be allowed to exist on the lake. There are signs that a permanent sudd vegetation will develop in such areas, associated with some plants already present, such as *Vossia* or *Scirpus cubensis*, or some plant yet to make its appearance, such as *Papyrus*, occurring naturally in the Okovango Swamps of Bechuanaland which partly drain into the Chobe swamps upstream of the Victoria Falls. In this respect it is very curious that *Eichornia crassipes*, has not yet put in an appearance on the lake, where a very careful watch is kept for it.

If an extensive infestation reaching along virtually the whole of the Zambezi system is allowed to persist, it must constitute a permanent threat to the rest of tropical and sub-tropical Africa, and to further developmental projects such as the Volta scheme in Ghana. A timely reminder of the uncanny ability of *Salvinia auriculata* to achieve long-distance dispersal, despite rigorous precautions aimed at preventing this, is its recent spread in 1962 to the Prince Edward Dam, a water reservoir on the outskirts of Salisbury, over 200 km. from Lake Kariba and some 1,000 m higher in altitude.

For the biologist, *Salvinia auriculata* emphasizes how little we yet know of the processes by which relatively innocuous native plants, removed from their natural habitat to a new one, achieve there an explosive rate of reproduction and an overwhelming colonizing abiltty. Nor do we yet know by what stages of evolution the present floating vegetation of African natural waters was developed.

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LIST OF VASCULAR PLANT SPECIES FOUND GROWING IN SUDD ON LAKE KARIBA

Ageratum conyzoides L.
Alternanthera nodiflora R. Br.
Basilicum polystachyon Moensch.
Cissampelos mucronata A. Rich.
Commelina diffusa Burm.
Cyperus articulatus L.
C. auricomus Sieber
C. denudatus L.
C. dives Del.
C. flabelliformis Rottb.
C. longus L.
C. nudicaulis Poir.
C. sphaerospermus Schrad.
Diandrochloa namaquensis (Nees) Stapf
Echinochloa pyramidalis Hitchcock et Chase
Eclipta alba L.
Equisetum ramosissimum Desf.
Hibiscus diversifolius Jacq.
Hyparrhenia dichroa (Stapf) Stapf
H. rufa (Nees) Stapf
Kyllingia alba Nees
Ludwigia adscendens (L.) Hara
L. erecta (L.) Hara
L. leptocarpa (Nutt.) Hara
L. pubescens (L.) Hara
Mariscus dubius (Rottb.) Kukenth.
Panicum maximum Nees
Phragmites mauritianus Kunth
Pistia stratiotes L.
Polygonum salicifolium Brouss.
P. tomentosum Willd.
Pycreus mundtii Nees
P. polystachya Beauv.
Rhynchospora corymbosa Domin
Scirpus cubensis Poepp. & Kunth
Sphaeranthus incisus Robyns
Typha australis Schumach.
T. capensis Rohrb.
Vigna sp.
Vossia cuspidata (Roxb.) W. Griff.